THE INHERITANCE OF COAT COLOR IN HORSES

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IN May, 1912, I published a paper on "The Inheritance of Coat Color in Horses." It was based on a study of the American saddle horse. I knew at the time of my investigation that A. H. Sturtevant, of Columbia University, N. Y., had in the hands of the printer a manuscript which gave a summary of all papers published to date on the subject. It was my agreement with him, made at Cold Spring Harbor, N. Y., in 1911, that when his paper was published I was to draw on its material for another summary of the problem involved. Sturtevant's paper, "A Critical Examination of Recent Studies on Colour Inheritance in Horses," was published in the *Journal of Genetics,* Vol. II, No. 1, Cambridge, England.

Sturtevant had published, August, 1910, in the *Biological Bulletin,* his study of the "Inheritance of Color in the American Harness Horse." Hurst, of England, had based his conclusions on a study of the English thoroughbreds. Wilson had tabulated the color of the Shire, Clydesdale and thoroughbreds; while Harper had given his attention to the French percherons. To these five breeds I am now able to add the records of the saddle horse. It is my purpose to combine the figures and draw some conclusions from them.

My apology, if one be necessary, for devoting so much time to the color of the horse is, that this is only a part of a larger study, the determination of the unit characters of the horse. I hold that we can make poor progress in this larger work until we have solved the most obvious ones of these characters. If there is a law governing the transmission of color, may we not infer that a law of somewhat like nature will govern the transmission of the more essential qualities of the horse? If it can be proved

that colors are unit characters and their inheritance obeys the Mendelian Law of dominants and recessives, I believe one very important step will have been taken to solve the whole problem of breeding horses.

This problem of breeding horses is a very large one. No other animal is quite so valuable as the horse. Immense sums of money are invested in farms and studs for his production. The value of the horses themselves mount up to over a thousand million of dollars. In number the horses in this country are over twenty million. The large farmers may have automobiles, engines and other mechanical devices, but they have horses and use them in large quantities. The small farmer's most valuable possession is the faithful family horse. Yet, how little is known about the scientific breeding of this valuable animal. Hogs and cattle we are producing to order, but the production of the horse is still a haphazard business. I believe that any effort that will aid the breeder in producing better horses will be an effort well spent.

In going through the American Saddle-Horse Register I secured the color in 3,913 matings, which involved the color of 11,739 horses. To these numbers I am now able to add from Sturtevant's tables 8,464 matings, giving a total of 12,377 matings or the color of 37,131 horses. This number is sufficiently large, it seems to me, to enable proper deductions to be drawn, unless it is in the case of the rare colors.

The tabulated matings and the resulting foals are:

Chestnut × Chestnut

Breed	Chestnut	Black	Brown	Bay	Authority
Thoroughbred.....	1095	9 (bay or brown)			Hurst
Shire.....	44	1	1	5	Wilson
Trotter.....	69	0	0	0	Sturtevant
Saddle.....	224	0	0	0	Anderson
Total.....	1432	16 not chestnut			
	99%	1%			

Chestnut × Black

Saddle.....	77	52	13	98	Anderson
	32%	22%	6%	40%	

Chestnut × Brown

Saddle	44 24%	24 12%	23 12%	102 52%	Anderson

Chestnut × Bay

Saddle	318 34%	36 4%	27 3%	536 59%	Anderson

Black × Black

Percheron	0	49	2 not black		Harper
Shire	2	39	0	3	Wilson
Clydesdale	0	36	2	0	Wilson
Trotter	2	34	4	2	Sturtevant
Saddle	5	114	4	0	Anderson
Total	9 3%	272 91%	12 4%	5 2%	

Black × Brown

Thoroughbred	0	8	20	12	Wilson
Shire	4	39	36	19	Wilson
Clydesdale	1	61	106	34	Wilson
Trotter	1	11	9	5	Sturtevant
Saddle	6	69	38	40	Anderson
Total	12 2%	188 35%	209 42%	110 21%	

Black × Bay

Thoroughbred	14	1	27	33	Wilson
Shire	19	39	43	125	Wilson
Clydesdale	7	40	67	104	Wilson
Trotter	7	16	31	48	Sturtevant
Saddle	54	141	77	261	Anderson
Total	101 9%	237 22%	245 21%	571 48%	

Brown × Brown

Breed	Chestnut	Black	Brown	Bay	Authority
Thoroughbred	11	6	114	78	Wilson
Shire	2	7	27	20	Wilson
Clydesdale	0	32	165	34	Wilson
Trotter	0	5	7	7	Sturtevant
Saddle	0	12	19	14	Anderson
Total	13 2%	62 11%	332 59%	153 28%	

Bay × Brown

Thoroughbred	123	10	365	744	Wilson
Shire	5	23	56	133	Wilson
Clydesdale	5	25	254	206	Wilson
Trotter	8	9	31	81	Sturtevant
Saddle	25	47	85	223	Anderson
Total	166 7%	114 5%	791 32%	1387 56%	

Bay × Bay

Thoroughbred.....	270	1	125	1295	Wilson
Shire.....	28	13	18	287	Wilson
Clydesdale.....	5	6	59	243	Wilson
Trotter.....	9	1	3	46	Sturtevant
Saddle.....	122	58	58	660	Anderson
Total.....	434	79	263	2531	
	13%	2%	8%	77%	

Gray × Not Gray

	Gray	Not Gray	
Thoroughbred.....	73	56	Wilson
Shire.....	146	186	Wilson
Clydesdale.....	9	15	Wilson
Trotter.....	141	142	Sturtevant
Saddle.....	49	89	Anderson
Total.....	418	488	
	46%	54%	

Gray × Gray

All breeds.....	47	18	
	72%	28%	

Chestnut	Black	Brown	Bay	Gray	Roan
9	2	2	9	1	13

Roan × Black

1	11	3	1	0	15

Roan × Brown

1	5	16	18	1	28

Roan × Bay

9	5	12	38	1	50

Roan × Gray

0	0	3	0	5	7

Roan × Roan

0	0	0	3	2	9

It will be seen from the foregoing that out of 1,438 matings of chestnut with chestnut all the foals are chestnut except 16. Sturtevant gives from 69 such matings all chestnut foals. In like manner I report 224 chestnut matings producing chestnut foals. This makes a total of 293 foals from chestnut matings among the two

breeds, trotter and saddle horse, without an exception. It is true that I found in the records two bay colts reported from chestnut sire and dam. The breeder of them is still living and informs me that it is a typographical mistake in the record. I have made diligent effort in the last few months to find a living colt from chestnut parents that is not chestnut itself. My efforts have been in vain, although I have asked in the breeding journals for the information so as to give it the widest publicity.

I have no doubt that either mistakes in the record or in the reports for registration are numerous enough to account for the 16 exceptions given in the above tabulation. There are those chestnut horses whose color is so close to that of a light bay that it would be marvelous if mistakes were not made in reporting the color for registration. Then, too, it is not always easy to determine the color the horse is to be by examining the young foal. As a rule the colt that has the dark mane and tail and dark legs will shed out to be a bay, while that one which has the light mane, tail and legs will shed to be a chestnut.

There is a tendency to blend in bay and chestnut. While the blend is not complete by any means, its tendency is apparent and at times gives trouble to foretell the color of the mature horse. I have examined a bay stallion that had on his ankle a small space covered exclusively with chestnut hairs. It is these animals on the border line that are so liable to be registered bay when in fact they are chestnut. I find numerous errors in all the registration records which I have been able to examine. The color of the horse has always been a minor consideration in registration, the pedigree being considered the important thing. Often the pedigree is mutilated by typographical mistakes. Why should we not expect the color to be changed in the same way?

The other writers on this subject have not given any figures showing the behavior of chestnut when mated to bay, brown and black. I find that black to chestnut gives: 32 per cent. chestnut, 22 per cent. black, 6 per cent. brown, and 40 per cent. bay. Brown to chestnut gives: 24 per

cent. chestnut, 12 per cent. black, 12 per cent. brown, and 52 per cent. bay. Bay to chestnut results in: 34 per cent. chestnut, 4 per cent. black, 3 per cent. brown, and 59 per cent. bay. The behavior of bay with chestnut is just what is to be expected if chestnut is recessive, as it seems to be. But it is in the matings of chestnut with black and brown that the real difficulty is encountered. Why should chestnut and black matings give 40 per cent. bay, and with brown it gives 52 per cent. bay. I must confess that up to this time I have not found an explanation to this. With these exceptions chestnut certainly behaves as a recessive to all other coat colors in horses.

Another strong evidence of the hypostatic position of chestnut is found in the matings in which it is not involved in the color of either the sire or the dam. Black $\times$ black matings give 3 per cent. chestnut foals. Black $\times$ brown gives 2 per cent. chestnut. Black $\times$ bay gives 9 per cent. chestnut. Brown $\times$ bay gives 7 per cent. chestnut. Brown $\times$ brown 2 per cent. chestnut. Bay $\times$ bay gives 13 per cent. chestnut. Here are six classes of matings with no external evidence of chestnut in the animals mated, yet regularly there come from them chestnut foals. This certainly is the way a unit-character should behave, and to behave this way it must be recessive. A striking example of the recessive nature of chestnut is to be found in The Theorist, a chestnut trotting bred stallion. I gave his color pedigree in *The Horseman* of December 17, 1912. The three generations immediately before him are of solid colors other than chestnut. The fourth generation has one chestnut individual, and the next generation two. If this is not the behavior of a unit-character I am unable to state how a recessive character should behave.

There are some stallions that are homozygous for their own colors and are unable to produce even from chestnut mares any chestnut foals. The two trotting stallions are Bingen and Alcyo, who, I have found, do not produce any chestnuts, although each one has had numerous mares who to other stallions do produce chestnut foals.

Black is dominant to chestnut and hypostatic to brown,

bay, gray and roan. The percentages are from a total of 298 black × black matings: 91 per cent. black, 3 per cent. chestnut, 4 per cent. brown, 2 per cent. bay. The brown and bay from black matings are very small, not enough to vitiate the conclusion that black is hypostatic to these two colors as well as to gray and roan. Under the present methods of registration there can be no sharp line of demarcation between black and brown. I am confident that as the records are now made up enough errors have crept in, by registering browns black, to account for the exceptions above mentioned. From true black horses mated to true black only black and chestnut will be obtained, in my opinion. The percentages of black colts from the cross of black and brown and black and bay are 35 per cent. and 22 per cent., respectively; just about the figures that the Mendelian law would justify.

In regard to brown and bay no little difficulty is encountered. Wilson says:

> The relative positions of bay and brown remain to be settled; and although there is evidence in favor of brown being dominant to bay, this conclusion is not clearly established. It must be remembered these are the colours breeders have the greatest difficulty in discriminating; and errors effect sires and dams and foals. In regard to sires it has been possible to correct the registered colors in several cases; and while every correction has increased the evidence in favor of brown being dominant, it is still possible there may be other explanations, as, for instance, that bay is a diluted brown.

Wilson's conclusion is that brown is dominant to bay, although he expresses a doubt as to the correctness of his own conclusions.

In his interpretation of the figures, Sturtevant goes the line of least resistance. He says:

> I am unable to agree with Wilson that bay and brown can satisfactorily be separated I base this upon my own observation, upon the frequent changes from bay to brown and *vice versa* which he (Wilson) mentions finding in the Clydesdale records, and the similar changes which I have observed among Harness Horse records, and upon the frequent recording of English Thoroughbreds as "bay or brown." My conclusions, then, are that brown and bay are not distinct, brown being merely a dark bay.

I do not believe that either Wilson or Sturtevant is correct. I reached the conclusion in my first paper, based on the records of the saddle horse alone, that brown is dominant to chestnut and black and hypostatic to bay. With all the figures before me now, I am still of the opinion that brown is recessive to bay. When bay is mated with brown the product is: 56 per cent. bay, 32 per cent. brown, 5 per cent. black and 7 per cent. chestnut. The total number of horses produced by this mating is 2,460, a number large enough to show that the percentages can be relied upon. Bay $\times$ bay produces: 77 per cent. bay, 8 per cent. brown, 2 per cent. black and 13 per cent. chestnut.

Brown $\times$ brown gives: 2 per cent. chestnut, 11 per cent. black, 59 per cent. brown and 28 per cent. bay. It is this 28 per cent. bay that is the greatest obstacle in the way of the interpretation which I have given to the results. If brown is a recessive to bay there should be no bay foals from brown sire and brown dam. Yet such matings yield a large per cent. of bay. I spent much time during the summer of 1912 studying the color of horses in the field. I believe that I have found an explanation for the above difficulty.

There is a brown horse that is called by horsemen the seal brown. The seal-brown horses appear to be almost black, and can easily be mistaken for black. The top line is all black, as is the mane and tail. The legs, except for possible white markings, are black up to the body. The body is very dark brown, in some cases showing a lighter shade near the flanks, and back of the nostrils a little of the lighter shade of brown is found. This is the true brown horse and only such should be recorded as brown.

There is a class of so-called brown horses known as the mahogany browns. These horses have black mane and tail, black legs, the top line of the body and sometimes the under line are black. The sides of the body have many bay hairs mingled with the black hair. Some blotches, usually near the flanks, seem to be exclusively bay. It seems to me that this horse is on the border line

between bay and black, or is an example of the incomplete dominance of the bay over the black.

If this theory be true, such mahogany brown horses are not, from the standpoint of reproduction, brown at all. No true brown foals should come from them unless the factor for brown be latent in their germ cells. They are examples of the simplex bay and when mated should give bay and black foals.

When it is remembered that the records have all these so-called mahogany browns recorded as browns, and no possible way to separate them, it becomes a very difficult matter to properly interpret results. I should be inclined to agree with Sturtevant that no separation of brown and bay can be made, were it not that I have found these two classes recorded as brown, while one class is a brown and the other class is a bay. Brown × brown matings, when a per cent. of genetically bay individuals enter into such matings, would have to give some bay foals. Twenty-eight per cent. of bay foals is none too large to expect from the number of simplex bays recorded as browns.

Another solution of this matter of black, bay and brown was suggested by A. B. Cox in a letter to me under date of May 14, 1912.

> Might it not be possible that bays, browns and blacks should be considered as a unit and that their appearance could be controlled by an independent factor; something on the same principle of the dilute factor in rabbits' color as set forth by Professor Castle? We have different shades of chestnut and also of gray roans, might not these different shades also be controlled by this dilute factor? Should we not divide the colors in three classes: (1) Gray roans; (2) bay, brown and black; (3) chestnut of different shades? Each class to be controlled by one factor, and then the different shades of these units to be controlled by an independent factor.

It is no little temptation to adopt this short series as it relieves at one stroke so many difficulties. Black, (seal) brown and bay are just as distinct colors as are chestnut and gray. This being so, I believe that each must have a separate factor, even though it may make the factors for color very numerous in the germ cells. For example, from gray × bay matings there are produced gray, bay,

brown, black and chestnut, five colors; showing that in the germ cells of a gray horse there must be the factors for five colors. In view of all the evidence which I have I adhere to my first interpretation, adopt the long series and place brown recessive to bay. Bay I place between brown and the two colors which are dominant to it, gray and roan.

That gray and roan are dominant to bay there can be no doubt. Nine hundred and six foals from matings gray $\times$ not gray produce 46 per cent. gray and 54 per cent. not gray. It is known that homozygous gray when mated with any of the four popular colors will always produce a gray. It is only from a heterozygous gray that other than a gray can be produced. Roan behaves exactly the same way. I have no records that would indicate the comparative strength of roan and gray. For the present I place them at the top of the series as of coordinate strength. It is just possible that there is a white that is dominant to both the gray and roan, but this has not come under my observation. Nor do I have any data to enable me to place dun in a series.

The cause of the different shades of roan, bay and chestnut must be left to another paper, as well as the interesting behavior of the white markings to be found on most horses, and also the dappled condition of certain grays, bays and chestnuts.

Sturtevant has suggested that *C* represent the factor for chestnut; *H* for black; *B* for bay (or brown); *G* for gray; *R* for roan, and *W* for white. I now suggest this change: Add the factors for brown, *Br,* and dun, *D,* and change black to *Bl.* The series then becomes: *C,* hypostatic to all others. *Bl* epistatic to *C* but hypostatic to *Br,* which in turn is hypostatic to *B.* *G* and *R* are both epistatic to *B,* and perhaps are hypostatic to *W.* This leaves *D* (dun) unplaced except that it is known to be near the top of the series with *G* and *R.*